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BIOSYSTEMATICS OF *SISYMBRIUM IRIO* COMPLEX XIII: TAXONOMIC CONSIDERATIONS

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ABSTRACT

After a brief discussion on the biosystematic principles in relation to the traditional taxonomy, the variation pattern of the *Sisymbrium irio* complex has been considered taxonomically. From a utilitarian point of view, the complex is divisible into two (diploid- hexaploid ; tetraploid- octoploid) species, although genetically there are four clear cut species. Such an arrangement is also in line with the genomic relations within the complex. For the present, it is proposed to treat the two members of each species as varieties. Only hexaploid matches with the Linnean holotype, and would thus get the name *S. irio* Linn. Pending a thorough search for synonymy within the species, a tentative scheme has been suggested.

INTRODUCTION

It is customary that a variation pattern, unravelled after any biosystematic investigation, should be recorded in the traditional taxonomic units. This has to be done with caution since the primary aims and objects of the traditional taxonomy have to be kept in view, and at the same time the true evolutionary relationships have to be reflected as accurately as is possible. Under such circumstances the conclusions of the various aspects of study have to be properly synthesized or intermeshed, which indeed is a difficult task.

The most important taxonomic unit is the species. Perhaps there is no other biological term which is so much debated that its meaning and scope have become a subject of great controversy. This indeed is inherent in the concept of species; since species, as we know now, are dynamic units and are found at all stages of evolutionary differentiation. Among others this aspect has been brilliantly brought out by the illuminating work of Clausen, Keck and Hiesey (see Clausen 1951). There is now a realization that an inclusive definition of species, which would hold good for all types of plants, is not even a theoretical possibility (*see* Gates 1950; Rollins 1952).

Since the advent of experimental approach, the species concept has become *apparently* more confused because sometimes the conclusions from the experiments do not fit well with the morphological concept of species. The most debated criterion of the species relationship is incompatibility and hybrid sterility. While all taxonomists acknowledge the importance of this criterion in maintaining the species as distinct taxa, most of them, however, do not agree that it should be the only criterion or even the major criterion for delimiting the species. Turrill (1936) has rightly concluded that if incompatibility and hybrid sterility is used as the primary criterion, it would result in a classification which, no doubt, would be natural but would not have a utility basis and would, therefore, serve the need of a specialist on the group. A routine 'utilitarian' type of classification would result only when morphology has been paid a due regard.

Strangely enough, in spite of this controversy, a perusal of the pertinent literature shows that often a classification based on biosystematic criteria ends nearly the same as the one on traditional taxonomic criteria, if these are used properly. This is because no competent biosystematist uses the criterion of incompatibility as all important and in fact, many view points are taken into consideration.

While taxonomists in general should imbibe data from the newer trends, the attitude of the experimentalists also needs moderation. There is a general trend that intraspecific polyplotypes found in nature should be elevated to species status, even if the differences are rather small. This line of thinking has been extended by Sakharov (1946) to the experimental auto-tetraploids of buckwheat. He suggests that because of the "lack of crossability and double chromosome number, it is considered that the tetraploid form can be given specific rank". However, polyploidy and species status need not be irrevocably tied together. Each case should be decided on its own merits. We do have examples where biosystematists have included polyplotypes in the same species as their progenitors because there are no outstanding differences between them: *Madia gracilis*—Clausen, Keck and Hiesey 1945; *Dodecatheon*—Thompson 1953; *Microseris*—Chambers 1955 etc.

The present writer agrees with Löve (1951) that in the strictest sense natural polyplotypes are seldom (if ever) absolutely like their parents in all their quantitative and qualitative characters. Nevertheless it has to be admitted that often the differences may be too small and only quantitative in nature. Such differences are of academic interest and Löve (1951) himself acknowledges that a "floristically untrained eye" cannot decipher these. Löve argues further that polyplotypes should not be given an intraspecific status because of the existence of a barrier. On this reasoning, according to him, polyplotypes should be elevated to a species rank. He draws indirect support for his view from the fact that most of the polyplotypes of North European plants had been given a specific status by older taxonomists. For one reason or the other, subsequent taxonomists found it wise to submerge these in the parental species. As Löve himself accepts, it is only possible in the flora of Northern Europe which has been critically analysed since the pre-Linnean times. On the other hand, there is a slight possibility of polyplotypes having been recognised as species in the floras of other countries in Africa and Asia, which have yet to be subjected to a critical analysis.

Taking all facts into consideration, one may reasonably conclude that there are two major attributes of species distinction, a proper measure of morphological dissimilarity and genetic incompatibility. The latter is certainly important when two or more than two species of a genus coexist. With this as the background, the present writer suggests that those polyplotypes should be given only an intraspecific status, whose difference with their parents is less in magnitude than the usual differential used for specific delimitation of that particular genus. The reason is that such polyplotypes have as yet achieved only one of the two chief attributes namely the genetic (and not the morphological) distinctness. Evidently such polyplotypes would, no doubt, constitute cryptic, incipient or genetic species because of the presence of a barrier to crossability. There is, however, one lacuna in this suggestion, that by definition and also by implication there should be no barrier among the members of one and the same species.

On the other hand, those polyplotypes which show differences to about the same extent as the various species in a genus should be accorded outright a specific status. Of course it is understood that in all such cases there exists a genetic barrier between the polyplotypes and the parents.

STATUS OF THE RACES

It is broadly with the above view in mind that the present writer proposes to consider the taxonomic aspect of this complex. At the very outset it should be admitted that in *Sisymbrium*, and in fact in entire Cruciferae there is, a general lack of outstanding differences distinguishing not only species within a genus, but often genera also. Among other points one of the chief causes for this is that mostly *Sisymbrium* is a self-pollinated genus. As a result of this, flower structure is so similar in details of dimension, structure, nectaries, colour etc., that it is hardly of any value in classification. Grant (1950) has already indicated that the genera which are bee-pollinated show comparatively a wider variation in flower structure in contrast to the self-pollinated flowers which have a rather stereotyped flower structure in various members of the genus. Rollins (1941) has also pointed out that relatively small and "trivial characters have to be elevated as species distinctions and relationships in *Arabis*" (Cruciferae). The same is applicable to *Sisymbrium* where the differential for species distinctions has to be of a lesser magnitude.

It has been shown by the writer (Khoshoo 1958a) that in nature, there is an intricate series of modifications in plant body of the members of this complex. This arises due to a similar intricate mixture of habitat factors. The modifications add to the already existing taxonomic difficulties of the complex. The experiments on modifiability have amply confirmed that in general there is a lack of absolutely outstanding taxonomic criteria in *S. irio* complex. Furthermore, these studies have also shown that the following characters may be treated as "constant characters" since these are not modified: branching pattern; flower and its parts; siliqua; texture, breadth, size of style, pedicel breadth; and pubescence; the amount of pubescence may vary, but this character is useful when used against glabrous condition.

There is another set of characters which in the strict sense are modified, but the same peak is registered under most of the environmental conditions. In other words modifiability is only within certain recognizable limits. Such characters are: Pedicel length; siliqua length and seed size.

In general it may not be possible to distinguish the races on the basis of a single character and in such cases it is always worth while to consider groups of characters of a qualitative nature.

As referred to earlier, more often evidence from the various aspects of the study do not corroborate with one another. This is aptly true of the *irio* complex. Phylogenetically, the entire complex is a single unit along with the unknown diploid (BB) species (Khoshoo 1965). Morphologically the complex contains two distinguishable units: diploid-hexaploid and tetraploid-octoploid. Chiefly on reasons of incompatibility and hybrid sterility there are four (2x, 4x, 6x and 8x) clear cut units in a genetical or biological sense. Genecologically these four entities show cenospecific relationship since there is no gene exchange between them. On the basis of present distributional evidence only two (2x and 4x) are widely distributed out of the four races (Khoshoo 1966). The other two (6x and 8x and particularly the latter) are nearly fortuitous attempts which have arisen here and there within the wide range of the species. Furthermore, as will be evident presently, from the view point of taxonomic history, the hexaploid should be the chief unit to be included under *Sisymbrium irio* Linn. since the Linnean holotype appears to match favourably with the hexaploid race.

Keeping in view all the above arguments, the writer upholds the conclusion of the morphological view point, and as such the complex is divided into two units. In view of the fact that there are no sharp taxonomic criteria the writer feels that, in general, morphological evidence is complete for recognising the two units as two distinct species. One species should include diploid (AA) and hexaploid (AA A_1A_1BB), and the other should include tetraploid ($2A_12B$) and octoploid ($4A_14B$). This arrangement would also have the advantage of reflecting the resemblances in genomic constitution. In the first species there are taxa with either only A genome (2x) or its preponderance (6x). In the second species A and B genomes are in equal proportion. Naturally on this account there is expected to be morphological affinity among the members of each species. In the first species, distinction among the two members is possible because of the presence of B genome in hexaploid, but the members of the second group differ chiefly in grade of polyploidy which gives distinctions of a detailed nature only. Keeping this in view, we may propose that the members within these species be treated as varieties, even though under the terms of definition of a variety, gene exchange is possible. On the other hand, we know that such is not the case here. These intra-specific entities cannot be treated as subspecies because that may imply different geographic subdivisions within the total range of the complex. The rank of 'forma' is rather too low in view of the morphological and overwhelming cytogenetic evidence.

The exact taxonomic nomenclature of these entities is rather an intricate issue because it involves unearthing of relevant synonymy etc. However, a few points need emphasis.

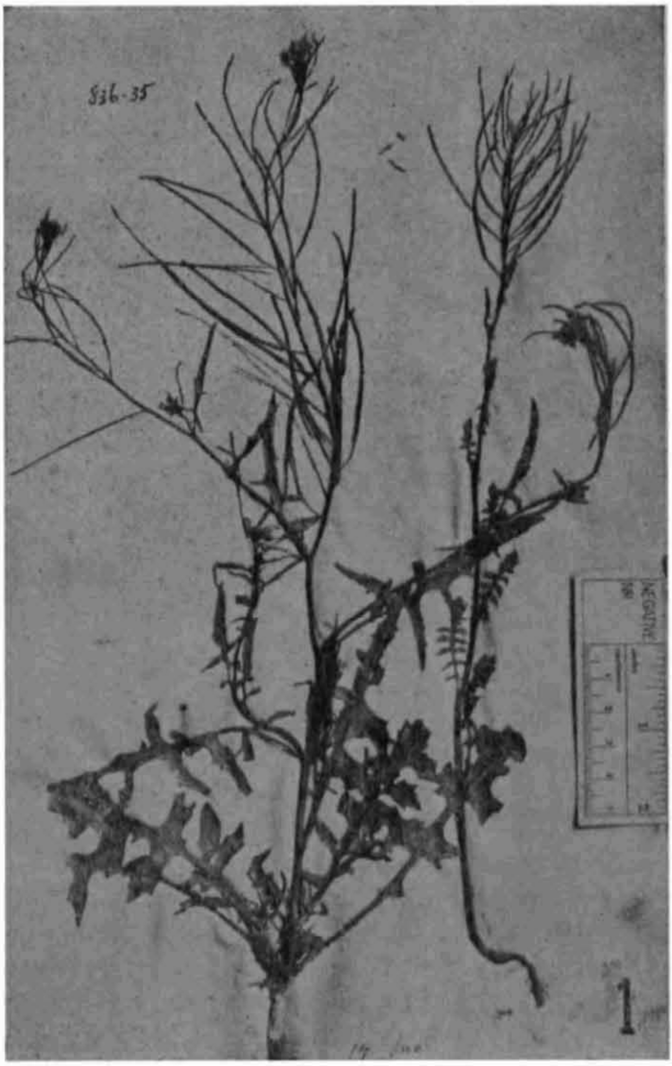

Fig. 1 : *Sisymbrium irio* Linn. Linnean Holotype (836·35)

Sisymbrium irio is a Linnean species and it was therefore imperative to compare all these races with the holotype lodged in the Linnean Herbarium (London). Mr. N. Y. Sandwith (Kew) very kindly undertook to make the comparison. The type sheet (836.35) contains two specimens (Fig. 1) which were collected from Spain. The larger specimen is thought to be the holotype. This will be considered first.

It possesses a main stem with 4 branches and is very much like the diploid or hexaploid. The leaves possess fewer lobes than any of the races seen in India. This, according to Mr. Sandwith, is also true to Spanish specimens in Kew Herbarium, and may be either a genic character or the result of modification due to habitat. The leaves are pinnatisect, possess lobules, lobes are dentate and, what is more important, they are lax. All these points are strongly suggestive of its being hexaploid rather than diploid. The young fruits do not overtop the flowers indicating that it is either diploid or hexaploid. The length and breadth of silique and pedicels tally very well with the hexaploid. This is further confirmed by the presence of indumentum on the pedicels and inflorescence axis as seen by Mr. Sandwith. Taking all facts together, the holotype is either diploid or hexaploid, perhaps the latter.

The smaller specimen differs in having silique which overtop the flowers. This is a tetraploid character. That, it is not a tetraploid, is clear from the pinnatisect leaves with dentate margins and silique and pedicels, which though still young are longer than the tetraploid. It is likely that this specimen was collected from a drier situation and therefore is diminutive. That it is so, is clear from the comparison of this plant (Fig. 1) with the diploid from dry-shade habitat (Khoshoo 1958a ; Plate VIII, Fig. 9). This comparison though not exact, nevertheless, reveals how dryness reduces the size of an individual in *irio* complex.

In conclusion, pending a detailed comparison particularly of size of flower parts, pollen* and seed, it appears that the Linnean holotype may perhaps be hexaploid, at any rate it is absolutely certain that it is a member of the first species (diploid-hexaploid). Therefore, the name *Sisymbrium irio* Linn. is applicable to the first species and in the strict sense perhaps only to the hexaploid. The hexaploid may have to be designated as *S. irio* Linn. var. *irio*, while the diploid could be designated by a name stressing its glabrous or subtorulose character of its fruit. The other species (tetraploid-octoploid) could be designated as *S. microflorum* stressing the small sized flowers or a name which would stress the characters of its fruit (firm, short and thick) as against the fruit of the first species (pliant, long and thin). The tetraploid race would constitute the typical element of this species, from which the octoploid could be distinguished on the basis of its much smaller fruit (*brevisiliqua*). A varietal rank can be suggested for the octoploid with considerable diffidence, since discovery of just four plants of this race is too small a population for such a purpose.

The following tentative key is presented for purposes of identification:

A. Main stem possessing a lower vegetative portion and ending at the top in flowering shoot. Branches in upper half. Leaves generally pinnatisect, lobes always dentate, lobule present. Petals distinctly longer than sepals. Petals 3-5 mm long. Tip of stamens acute or nearly so. Silique long (4.5 cm) pliant or nearly so......*S. irio* Linn. (sensu stricto)
    a. Plants glabrous; silique subtorulose, 0.75 mm broad; style 1 mm long; pedicel 0.25 mm broad ....Diploid.
    b. Plants pubescent; silique not subtorulose, 1-1.25 mm broad ; style 0.5 mm long ; pedicels 0.75 mm broad ....Hexaploid.

B. Main stem may or may not have lower vegetative portion. In all cases ends in a flowering shoot. The stem branches throughout when main stem has a lower vegetative portion. Leaves generally pinnatipartite or fid. Lobes dentate or dentate-sinuate. Lobule generally absent. Petals either just equal or smaller than sepals. Petals 2-3 mm long. Tip of stamens always obtuse. Silique short always less than 4 cms in length, firm ....*S. microflorum?*
    c. Lobes entire or sinuate-dentate ; silique more than 2-5 cm long, 1.25 mm broad ; style 0.25 mm ....Tetraploid.
    d. Lobes dentate ; silique at the most 2.5 cms long, 1.5 mm broad; style 0.75 mm ....Octoploid.

The above scheme of nomenclature is only tentative because all synonymy has yet to be unearthed critically. However, it only shows the broad outline of a workable taxonomic treatment of the complex. A taxonomic treatment of the complex conforming to the rules of nomenclature will appear in due course. Furthermore, species like *S. irioides* Boiss. have also to be examined. So far no authentic specimen of this species has been available to the writer. Late Dr. W. B. Turrill informed the writer that this species was described by Boisser from a collection made by Aucher Eloy and so far as he could ascertain, that is the only collection that has ever been made of the species, if it be such. According to Hooker and Thomas (1861), and

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*From the work of Nair and Sharma (1967) it appears that hexaploid is distinctive in pollen morphology. An investigation of the Holotype from this point of view may be rewarding.

Hooker f. and Anderson (see Hooker 1872) *S. irioides* has flowers and style double in size to that of *S. irio*. From the brief description given by Hooker and Thomas (1861), which contains no dimensions of the flower and fruit, it appears that *S. irioides* may as well be hexaploid or diploid. Schulz (1924) treats it as *S. irio* Linn. var. *irioides* (Boiss.) Schulz. The description given by him indicates that petals (4-6 mm) are as long as hexaploid, and the length of style (upto 1.3 mm) indicates its resemblance with octoploid.

Of interest are the general remarks on *S. irio* by Hooker and Thomas (1861). These authors mention that flowers are variable in size and are "sometimes very small", and style also varies in length. Keeping in view the fact that flower size is hardly modifiable, it appears that these authors did have a wide variety of material, perhaps covering the various races discussed in this work. The words 'very small' flowers indicate a significant character of the tetraploid race.

STATUS OF THE THREE TYPES OF TETRAPLOID

The three types of the tetraploid race though showing no difference in dimensions of flower, fruit and seed, are nevertheless distinguishable from one another on the basis of branching pattern, leaf shape, difference in time of germination, flowering and maturity and above all in their individual habitat preferences. The reaction of the two types (*caulis* and *subcaulis*) to various environmental conditions has been amply brought out (Khoshoo 1957, 1958a). These have almost contrasting habitat preferences, *caulis* is very well suited to moist-shady to sunny situations, while *subcaulis* has a wider range and can very well tolerate the arid conditions. These points were also fully confirmed by laying transects in edaphically diversified areas. The *acaulis* type has always been found in moist-sunny but grazed fields. The probable adaptive value of their branching pattern has already been indicated (Khoshoo 1957, 1958b). The three types are genotypically different from one another. The F_1 hybrids among the three types are fertile. However, it is not yet possible to comment on the exact nature of their genetic differentiation responsible for preserving their morphological and ecological differences.

The best taxonomic work on the genus is by Schulz (1924), who recognizes three varieties and six forms within *Sisymbrium irio* Linn. As indicated earlier an idea about the treatment of Indian forms could be secured by examining the herbarium material in Forest Research Institute (Dehra Dun), which has been identined by O. E. Schulz himself in 1925 and 1926 (Khoshoo 1966). It was indicated that forma *hygrophyllum* Fourn. is the same as *caulis* type of the present writer and forma *dissectum* Schulz is the same as *subcaulis* type. Furthermore, in all probability forma *minimum* Pourret is the same as *acaulis* type. Therefore, it appears that the three types have been already accorded an intraspecific status by earlier taxonomists. There are several instances when older taxonomists recognized intraspecific variation within widely distributed species and the later biosystematic work showed that these intraspecific units were either climatic or edaphic ecotypes. The classical example is by Turesson (1922) in *Hieracium umbellatum*. To quote an instance, forma *filifolium* Fr. of this species proved to be an ecotype due to arenaceous habitat. Same is also true of the various subspecies of *Potentilla glandulosa* as studied by Clausen, Keck and Hiesey (1940).

The question as to whether in the light of the above statements, the three local types should be regarded as three distinct ecotypes, cannot be answered with finality for more than one reason.

The ecotypic concept is as yet a controversial issue. On one hand are Turesson (1922), the author of the term, and Clausen, Keck and Hiesey (1940) who have been able to recognize ecotypes with some distinctness within several European and Western-North American species respectively. On the other hand, Gregor (1939) and his school have failed to find an evidence for clear cut ecotypes as conceived by the former school. Instead Gregor and his collaborators have found evidence for continuous variation and therefore the use of the term 'cline' (Huxley 1938) was suggested. Furthermore, the ecotypes of Turesson are both local and regional, while those of Clausen, Keck and Hiesey are regional, and, what is more important, are genetically heterogeneous. Turrill (1946) has remarked "that within regional ecotypes there may be other smaller, ecologically delimited groupings which would equally well conform to the definition of ecotypes. There would thus be ecotypes within ecotypes". Therefore, what the present writer may have discovered are only different biotypes within bigger regional groupings which have yet to be unravelled. As such a genecological status cannot be given to the three types particularly because the present writer has so far surveyed only a small area considering the entire range of distribution of this species (*see* Khoshoo 1966, Fig. 1).

On the other hand, Turesson (1922) found ecotypic variation in *Hieracium umbellatum* within a distance of only 35 km. If one were to follow this reasoning, the three types of tetraploid would be edaphic and biotic ecotypes. Apart from their physiological differences, these also differ in some morphological characteristics (Khoshoo 1958b), though morphological differentiation is not a prerequisite for classifying ecotypes. Ecotypes of *Achillea* have no morphological differentiation (Clausen, Keck and Hiesey 1948), while those of *Potentilla glandulosa* (Clausen, Keck and Hiesey 1940) have.

In conclusion it may be stated that a biosystematic or even a purely taxonomic treatment of the three types should be deferred until variation pattern is analysed on a broader basis. At the moment it is better to recognize these as three distinct biotypes.

CONCLUDING REMARKS

Some taxonomic considerations have arisen as a result of the study. These are presented here in a tentative fashion. In general, there are only small differences between species and also between genera of Sisymbrieae. Under such circumstances the value of biosystematic criteria for proper understanding of the taxonomic relationships is very great. Therefore, it would be worth while to extend this study to Sisymbrieae as a whole, since Rollins (1943) has also noticed a good deal of "tangle in generic relations". Even the genus *Sisymbrium* has been variously treated (*cf.* Bentham and Hooker 1862-1867; Schulz 1924). When genera, let alone species, are not based on precise and clear cut morphological differences, then relatively small characters have to be elevated to position of importance.

Same taxonomic conclusions do not emerge from the various aspects of the study of *irio* complex. The writer, after taking all facts into consideration, has come to the conclusion that for practical purposes the complex should be divided only into two species (diploid-hexaploid; tetraploid-octoploid). Such an arrangement would be in line with the genomic relations within the complex. For the present, it is proposed to treat the two members of each species as varieties, though strictly by definition and by implication of the term it is not a correct procedure, because in this case the varieties within the two species have a genetic barrier.

On comparison with the Linnean holotype, the hexaploid alone appears to match with it and would thus get the name *Sisymbrium irio* Linn. Pending a thorough search for synonymy within the species, a tentative scheme has been suggested. The herbarium material of the various races has been deposited in the herbaria of the Punjab University (Chandigarh) and National Botanic Gardens, Lucknow.

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